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Host plant use in the assemblage of herbivorous insects on *Macaranga* myrmecophytes

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Summary

Chapter 1. General Introduction

Ants are extremely abundant in terrestrial ecosystems, especially in tropical rainforests. Some plant species in various taxa of angiosperm in tropical areas are known to have evolved into myrmecophytes, which are defined as plants that have symbioses with ants through harboring the ants inside the hollowed domatia. The ants that have symbiotic relationships with myrmecophytes are called “plant-ants”, which usually defend the host plants from herbivores. The defense through ants is called “ant defense”. So far, it has been revealed that there are inter- and intra-specific variations in the modes and intensities of ant defenses among myrmecophytic species. Here, I hypothesize that, in response to the variations, herbivores on myrmecophytic plants have evolved various counter-adaptations to overcome such ant defenses, and that ant defenses affect the patterns of host plant use by the assemblage of herbivores on the myrmecophytes. The purpose of this thesis is to empirically explore how ant-plant mutualism on myrmecophytes affects the host plant use by the assemblage of herbivorous insects on sympatric myrmecophytic species. For the purpose, I focused on the genus *Macaranga* (Euphorbiaceae), which contains many myrmecophytic species in the Southeast Asian tropics.

Chapter 2. Study site and plants

This study was conducted in Lambir Hills National Park, Sarawak, Malaysia. The park is covered with primary lowland mixed dipterocarp forest. The climate of the area is aseasonal with 3000 mm of rain per year, and average rainfall is > 100 mm for all

months. Daily mean maximum temperatures are approximately 32℃. More the 15 *Macaranga* species, including twelve myrmecophytic species, are distributed in the study site. Their microhabitats frequently overlap each other in the opened habitats. The myrmecophytic species associate primarily with the genus *Crematogaster* ants, and the partnerships between *Macaranga* myrmecophytes and *Crematogaster* plant-ants are highly species-specific. The myrmecophytes provide their plant-ants with nutrient-rich food bodies and hollow stems. It has been demonstrated that there are variations in the starting time of symbiosis in plant ontogeny, the amount of investment by plants for plant-ants, and the intensity of ant defenses among myrmecophytic *Macaranga* species. There are considered to be an inverse relation between the intensities of ant and non-ant defenses in *Macaranga*. The plant-ants sometimes drastically decrease or disappear due to accidental disturbances or predation by predators.

Chapter 3. Patterns of host plant use in the assemblage of herbivorous insects on 15 species of *Macaranga*

To examine how the variation in anti-herbivore defenses among *Macaranga* species affect the host plant use of the herbivorous insects, I sampled herbivorous insects on 11 myrmecophytic and four non-myrmecophytic species of *Macaranga* in the field and reared some of them in the laboratory. At least 79 species of herbivorous insects belonging to at least 34 families were found to feed on the 15 *Macaranga* species. They comprised four feeding-habit guilds: guilds of leaf chewers (accounting for 48.1% of all the species), suckers (31.6%), gall-makers (17%) and leaf miners (2.5%). The leaf chewer guild was dominated by lepidopteran species (75%), followed by orthopterans (10%), phasmids (7.5%) and coleopterans (7.5%). All of the suckers, the gall-makers and the miners were hemipterans, dipterans, and lepidopterans, respectively. I found three features in the host plant use by the assemblage of herbivorous insects: 1) the herbivores feeding on ant-active individuals of myrmecophytic species tended to have much narrower host plant ranges, compared to the other herbivores, and seemed to be specialists that use one or a few closely-related plant species, 2) almost all of the herbivores feeding on ant-inactive individuals of myrmecophytic species were generalist herbivores, 3) more herbivore species was observed on species with more intensive ant defenses than on those with less intensive ant defenses, except for the species with most intensive ant defenses. These features

suggest that 1) specialist herbivores have developed adaptive traits to overcome ant defenses of their host plants, 2) generalist herbivores, most of which have not special adaptation to ant defenses on myrmecophytes, opportunistically use some myrmecophytes only when the plant-ants there disappear or become inactive due to environmental disturbance.

Chapter 4. Potential host range of myrmecophilous *Arhopala* butterflies (Lepidoptera: Lycaenidae) feeding on *Macaranga* myrmecophytes

Several species of *Arhopala* butterflies (Lepidoptera, Lycaenidae) are known to be specialist herbivores of *Macaranga*. This chapter aimed to experimentally determine whether anti-herbivore defences by plant-ants restrict the larval host plant ranges of three *Arhopala* species feeding on myrmecophytic *Macaranga* species and one *Arhopala* species feeding on non-myrmecophytic *Macaranga* species. I fed larvae of the *Arhopala* species with the leaves of five *Macaranga* species under ant-excluded conditions, to examine the potential host plant ranges. Under ant-excluded conditions, three *Arhopala* species, *A. amphimuta*, *A. dajagaka*, and *A. major*, survived to the pupal stage when fed species not used in the field as well as their normal host species. The results suggested that the presence of plant-ants at least partially restricts the host plant ranges of larvae of the three *Arhopala* species. In contrast to the three *Arhopala* species, larvae of *A. zylda* grew to the pupal stage only when they feed on their normal host plant species.

Chapter 5. Myrmecoxeny in *Arhopala zylda* (Lepidoptera, Lycaenidae) larvae feeding on *Macaranga* myrmecophytes

The herbivores that feed on ant-active individuals of myrmecophytic *Macaranga* are expected to have adaptive traits to elude plant-ants. Although *Arhopala zylda* is known to feed on myrmecophytic *Macaranga* at the larval stage, the adaptive traits were unclear. In this chapter, I demonstrated that *A. zylda* larvae showed myrmecoxeny; they had no stable association with the plant-ants on their myrmecophytic *Macaranga* host plants. Despite the presence of many plant-ants, *A. zylda* larvae were rarely attended or attacked by ants on their host plants. The plant-ants of three other myrmecophytic *Macaranga* species (non-hosts to *A. zylda*) also paid little attention to experimentally introduced *A. zylda* larvae. The myrmecoxeny seen in *A. zylda* is notable

among lycaenid larvae that feed on myrmecophytes, because almost all are obligate intimate myrmecophiles.

Chapter 6. Exploitation of food bodies on *Macaranga* myrmecophytes by larvae of a lycaenid species, *Arhopala zylda*

Larvae of *Arhopala zylda* are known to feed on food bodies produced by two *Macaranga* myrmecophytic species. In this chapter, I examined their feeding behavior in detail via field observations and rearing experiments in the field and laboratory. Larvae of *A. zylda* fed only on food bodies and not leaves during the first through third instars; during the fourth (final) instar, they ate both food bodies and leaves of the host plants. The larvae actively fed on food bodies on young leaves, which were always attended by many plant-ants. These results suggested that *A. zylda* larvae depend entirely on food bodies for food, except late in the final instar, and that the food body-feeding habit is associated with special traits that enable the larvae to evade ant aggression, which usually functions as an effective anti-herbivore defense for the host plants.

Chapter 7. Host-plant preference of two species of *Orthomeria* (Phasmida: Aschiphasmatini) feeding on *Macaranga* myrmecophytes

In this chapter, I examined two phasmid species, *Orthomeria alexis* and *O. cuprinus,* which are known to feed on *Macaranga* myrmecophytes. My observations revealed that each phasmid species relied on two closely-related myrmecophytic *Macaranga* species for its host plants in spite of their normal plant-ant symbioses and that there was little overlap between their host plant preferences. More *O. cuprinus* adults and nymphs were found on new leaves, which were attended by more plant-ants, than on mature leaves, while most adults and nymphs of *O. alexis* tended to avoid new leaves. *O. alexis* adults chose a non-host *Macaranga* myrmecophyte that was more intensively defended by plant-ants and was more palatable than their usual host plants almost as frequently as their usual host plant. The results suggested that the host plant range of *O. alexis* was restricted by the presence of plant-ants on non-host plants. The plant-ants of the host plants of the two phasmids attacked the phasmids when they meet the phasmids. Phasmids' behaviors that appeared to evade plant-ant attacks were described.

Chapter 8. General discussion

The results shown in the preceding five chapters suggest that the myrmecophytism between *Crematogaster* ants and *Macaranga* plants significantly affects the assemblage of herbivorous insects on the myrmecophytes, and that it has been diversifying the assemblage through the following two processes. First, the ant defenses on the myrmecophytes have enhanced morphological and behavioral adaptations to overcome or elude the ant defense in some herbivores, and consequently promote the evolution of specialist herbivores feeding exclusively on a few of the myrmecophytes. Secondly, the opportunistic use of myrmecophytes by generalist herbivores promotes the diversity of herbivore on myrmeocophytes. Because non-ant defenses on *Macaranga* myrmecophytes, probably due to their intensive dependence on ant defenses, are much weaker than many other plants, generalist herbivores are able to enjoy "palatable" myrmecophytes' leaves without any of ant and non-ant defenses when disturbances make the plant-ants considerably inactive. Because such disturbances constantly occur, "palatable" leaves are constantly available for the opportunists though the incidence rate is not so high. In conclusion, ant-plant mutualisms are strongly suggested to contribute to the species diversification in the assemblage of the herbivorous insects in the tropical ecosystems.